

***Ceratitis capitata*: Effect of host fruit size on the number of eggs per clutch**

P. T. McDonald & D. O. McInnis

Tropical Fruit and Vegetable Research Laboratory, Agricultural Research Service, USDA, P.O. Box 2280, Honolulu, HI 96804, USA

Keywords: oviposition, *Ceratitis capitata*, density, fruit size of host, clutch size

Abstract

A laboratory strain of *Ceratitis capitata* (Wiedemann) was presented with grapes, plums, apples and peaches for oviposition. Fruit diameter was highly correlated with the number of eggs/oviposition. Clutch size was 3.9 ± 0.3 for grapes (20 mm) compared with 14.0 ± 0.7 for apples (70 mm). When Parafilm®-enveloped whole peeled fruits and smaller spheres of fruit flesh were offered, fruit size proved more important than fruit type in determining egg clutch sizes. Ovipositions that required the puncture of fruit skin gave larger clutches than ovipositions through Parafilm or into punctured fruit.

Introduction

The Mediterranean fruit fly, *Ceratitis capitata*, is a widespread and prolific pest whose exclusion from areas of fruit and vegetable agriculture requires constant vigilance. The medfly has a wide host range including more than 250 fruits, nuts and vegetables (Hagen *et al.*, 1981).

The strategy used in foraging for oviposition sites and the manner in which the sites are exploited influence the survival of the fly's progeny. Host finding depends on the recognition of physical factors (Nakagawa *et al.*, 1978) and probably chemical factors as well (Prokopy & Roitberg, 1984). Oviposition is influenced by fruit volatiles, fruit size and shape, color and humidity (Féron, 1962; Sanders, 1962, 1968a, b, 1969; Tanaka, 1965). Oviposition behavior has also been reported to be affected by the origin of the fly population (Prokopy *et al.*, 1984).

The medfly marks its oviposition sites with an oviposition deterrent pheromone to prevent the over exploitation of fruits and to insure a more even distribution of progeny among the fruit resources (Prokopy *et al.*, 1978). While the number of ovipo-

sitions has been shown to be regulated by the oviposition deterrent pheromone, the possibility that the number of eggs in an individual clutch could be regulated has never been investigated.

This paper reports findings on the influence of fruit size on the clutch size of medflies.

Materials and methods

The mass-reared Hawaii laboratory strain colonized for over 300 generations was used for these studies. Females to be tested were allowed to mate until 5 days old and tested when 6–8 days. Groups of 15 females in 30-cm³ observation cages were presented with market ripe fruit(s) of a single type for 2 h. During this period a census of the number of flies on the fruit(s) was taken at 10-min intervals to establish an index of host finding. Ovipositions were recorded continuously throughout the observation period. Oviposition was a puncturing into the fruit flesh followed by an interval of at least 15 s in the pose of egg deposition. Fruits were stored at room temperature for one day after exposure and then the number of eggs in each oviposition punc-

ture was determined. The investigation proceeded in four stages. Further details for individual tests are given below.

Oviposition in various whole fruits. The following whole fruits were presented in the experimental cages: Thompson seedless grapes – 10 of 20 mm diameter, plums – 2 of 45 mm diameter, Golden Delicious apples – 1 of 70 mm diameter, and peaches – 1 of 80 mm diameter. Each test was replicated five times.

Oviposition in punctured fruits. Since flies sometimes oviposited into a preexisting puncture, performance with punctured fruit was evaluated. The following fruits were presented in the experimental cages: Golden Delicious apples – 1 of 70 mm diameter and Lady apples (crab-apples) – 2 of 35 mm diameter. Each test was replicated four times. In each trial one of a pair of cages had unpunctured fruit and the other held fruit with holes of 0.5 mm diameter and about 3 mm depth made with a probe. Holes were evenly spaced on the sides and numbered 24 for an apple and eight for each crab-apple. Observation time was reduced to 1 h.

Oviposition on whole fruits by individual flies. Single flies were exposed to either a grape (in 1 pint cylindrical cages of 8 mm diameter and 6 mm height) or an apple (in 30 cm³ cages). Each grape was removed and replaced immediately after being punctured. A single apple was used by each fly. Each puncture was sealed and designated by a coded 1-cm² piece of masking tape. Each test period was 90–120 min.

Oviposition in spheres of fruits. A technique established for *Rhagoletis cerasi* oviposition (Boller, 1968) was adapted to study the effects of different

sizes of the same fruit type. Whole apples (70 mm diameter) or whole papayas (85 × 120 mm) were peeled and enveloped in a taut covering of Parafilm®. Spheres (20 mm diameter) were carved from apple or papaya pulp with a melon baller and wrapped in Parafilm®.

The experimental cages contained either one whole fruit or four spheres of like type. Spheres were removed and replaced after a puncture. A single whole fruit was used throughout the observation period. Simultaneous presentations of whole fruits and spheres were terminated when ten punctures had accrued to either of the types. Each puncture was marked with a dot of red nail lacquer to prevent reuse by the fly (in the case of the whole fruit) and to facilitate detection of the stings. Simultaneous comparisons were conducted with 20-mm spheres of apple and papaya.

The data were analyzed using Student's t-test for paired comparisons and Fisher's L.S.D. test for groups of three or more means.

Results

Oviposition in various whole fruits. The responses of the laboratory-colonized medflies to the 4 fruits were variable. The flies were significantly less successful finding peaches and grapes than plums and apples (Table 1). The flies were observed ovipositing significantly less often on the peaches than on the other fruits. For all fruits the number of ovipositions exceeded the number of puncture sites. The total number of eggs deposited in peaches and grapes was significantly fewer than in the other fruits.

The flies showed a significant and consistent difference in eggs/oviposition for different fruits (Table 1). For the smallest fruit, grape, eggs/oviposi-

Table 1. Host-finding and oviposition behavior of *C. capitata* on four fruits.^{1,2,3}

Fruits	Diameter (mm)	Index:flies on hosts	No. ovipositions	No. punctures	No. eggs	Eggs/oviposition
Grapes	20	47.6 ± 6.6 b	66.2 ± 12.8 ab	14.2 ± 1.3 b	110.4 ± 23.7 b	1.7 ± 0.1 c
Plums	45	87.4 ± 10.6 a	81.0 ± 16.2 a	22.2 ± 4.0 a	352.0 ± 45.3 a	4.7 ± 0.4 b
Apples	70	84.0 ± 7.1 a	47.2 ± 6.6 b	14.4 ± 2.3 b	361.4 ± 51.0 a	7.7 ± 0.3 a
Peaches	80	37.0 ± 10.2 b	20.6 ± 5.6 c	10.8 ± 2.5 b	161.8 ± 42.8 b	8.2 ± 0.7 a

¹ Data are mean ± s.e.

² Within a test values in same column followed by same letter not significantly different by Fisher's L.S.D. or Student's t-test ($p < 0.05$).

³ Five replicates of each treatment.

tion averaged 1.7 ± 0.1 . The mean eggs/ oviposition value for the intermediate size fruit, plum, was intermediate at 4.7 ± 0.4 . For the large fruits, apple and peach, eggs/ oviposition averaged 7.7 ± 0.3 and 8.2 ± 0.7 , respectively. The correlation between fruit diameter and eggs/ oviposition was highly significant ($r = 0.996$, $p < 0.1$, $df = 2$).

Oviposition in punctured fruits. Puncturing significantly increased the incidence of oviposition and total number of eggs deposited in both apple and crab-apple (Table 2). The values of eggs/ oviposition were significantly smaller in the punctured fruits in each case. As in the previous experiment, the number of ovipositions observed exceeded the number of puncture sites.

Oviposition on whole fruits by individual flies. A total of 192 oviposition bouts was recorded, 108 for grapes and 84 for apples (Table 3). All observed ovipositions in apple resulted in egg deposition; however, only 75 of the 108 grapes yielded one or more eggs. For these 75 grapes, the clutches averaged 3.9 ± 0.3 eggs. The apples contained clutches with an average size of 14.0 ± 0.7 eggs. The means were highly significantly different by t-test ($p < 0.01$, $df = 157$).

Twenty-three females oviposited three or more clutches (Table 3). For both fruits there was a trend for subsequent egg clutches to be smaller than the

first, and for apples, the first clutch was significantly larger than the second ($t = 2.49$, $p < 0.05$, $df = 20$).

Oviposition in spheres of fruit. Simultaneous presentations of whole peeled apples (70 mm) or spheres of apples (20 mm) or whole peeled papaya (85×120 mm) and spheres of papaya (20 mm) were conducted. Because the puncture from each oviposition event was individually denoted and dissected, the clutch size from each oviposition was known. Results are in Table 4. Flies oviposited significantly larger clutches in whole papayas than in the papaya spheres. Likewise, they oviposited significantly larger clutches in whole apples than in the apple spheres.

Table 4. Clutch size of *C. capitata* ovipositing on Parafilm®-covered whole fruits and spheres.

Test	Fruit	Size (mm)	Total punctures	Punctures with eggs	
				No.	Clutch size ^{1,2}
I	Papaya	85×120	64	59	10.9 ± 0.7 a
	Papaya	20	80	57	6.1 ± 0.3 b
II	Apple	70	68	55	8.2 ± 0.6 a
	Apple	20	78	55	5.2 ± 0.3 b
III	Papaya	20	64	50	5.9 ± 0.4 a
	Apple	20	65	59	4.8 ± 0.3 b

^{1,2} See Table 1.

Table 2. Host-finding and oviposition behavior of *C. capitata* on whole and punctured (P) fruits.^{1,2,3}

Test	Fruit	Diameter (mm)	Index:flies on hosts	No. ovipositions	No. punctures	No. eggs	Eggs/ ovipositions
I	Apple	70	54.0 ± 1.6 a	18.0 ± 2.5 b	9.3 ± 1.4	182.0 ± 28.8 b	10.2 ± 0.9 a
	Apple, P	70	54.0 ± 2.3 a	49.3 ± 3.4 a	(24)	275.8 ± 36.4 a	5.7 ± 0.7 b
II	Crab-apple	35	41.8 ± 4.4 a	11.3 ± 3.1 b	3.3 ± 0.8	73.0 ± 24.8 b	6.3 ± 0.5 a
	Crab-apple, P	35	40.5 ± 7.4 a	67.8 ± 10.5 a	(16)	275.5 ± 50.7 a	4.0 ± 0.3 b

^{1,2} See Table 1.

³ Four replicates of each treatment

Table 3. Clutch size of *C. capitata* ovipositing in grape (20 mm diameter) and apple (70 mm diameter).^{1,2}

Fruit	Flies ovipositing 1× or more			Flies ovipositing 3× or more			
	No. flies	No. ovipos.	Eggs/clutch	No. flies	Eggs/ 1st clutch	Eggs/ 2nd clutch	Eggs/ 3rd clutch
Grape	30	75	3.9 ± 0.3 c	11	5.8 ± 1.2 c	3.9 ± 0.7 c	3.7 ± 1.2 c
Apple	40	84	14.0 ± 0.7 ab	12	16.1 ± 1.7 a	11.2 ± 1.0 b	13.8 ± 1.9 ab

¹ See Table 1.

² Values followed by same letter not significantly different by Fisher's L.S.D. test ($p < 0.05$).

The effect of different fruit content was investigated using the 20-mm spheres of papaya and apple (Table 4). The papaya spheres held clutches that were significantly larger than those oviposited in the apple spheres ($t = 2.2, p < 0.05, df = 107$). Nevertheless, the magnitude of this difference was much less than that for the different size fruits of the same type.

Discussion

A critical element in the survival of medflies, which often occur in dense populations, is the distribution of their progeny in many fruits so as to maximize fruit usage and minimize competition. In tephritids the prevention of intraspecific competition in limited resources of fruit is chiefly accomplished through the marking and detection of oviposition deterrent pheromones or the sensitivity to developing larvae within fruit (Prokopy & Koyama, 1982; Fitt, 1984). The regulation of egg deposition according to size of fruit and the ease of puncturing is another mechanism to promote the optimal distribution of progeny among the environmental resources.

To our knowledge this is the first report of a fruit fly adjusting the clutch size according to host fruit resources. Most likely this regulation limits competition and results in progeny of greater fitness. In the gall-forming midge *Asteromyia carbonifera*, the clutch size determines the fitness of the progeny (Weis *et al.*, 1983). In that case, optimal clutch size was determined by factors such as competition and parasitism.

The heaviest fruit infestation occurs under conditions of high fly density. In orchards on Maui, Hawaii, peaches support 50 larvae per 100 g of fruit under these conditions (Wong *et al.*, 1983). Smaller peaches were found to support smaller numbers of larvae than larger ones. Fruit quality was found to be as important to survival as biomass; e.g. citrus supported only about ten larvae per 100 g of fruit. Medfly larvae have been shown to have a wide discrepancy in growth and survival responses to different fruit pulps presented in the laboratory (Carey, 1984). Thus it is a definite advantage for flies to be capable of gauging the quality and quantity of the fruit into which their progeny are entrusted.

In several tephritid species, especially those using small fruits exclusively, only a single egg is normally deposited in each fruit puncture: *Dacus oleae* in olives, *R. pomonella* in blueberries, and *R. cerasi* in cherries (Christenson & Foote, 1960); and *D. latifrons* in chili peppers (authors, unpubl. obs.). Other species produce egg clutches of varying sizes: *D. cucurbitae* and *R. suavis* (Christenson & Foote, 1960); and *C. capitata*. The determiners of clutch size for other tephritids have yet to be defined, as does the response of populations specializing on small fruit within a species with a broad host range. The retention of a capacity to discriminate different fruit sizes by a strain colonized on artificial eggging devices for over 300 generations suggests a strong investment of *C. capitata* in egg clutch regulation, however.

Prior to oviposition there were agonistic encounters between females on a fruit, and these undoubtedly resulted in a lower oviposition activity level. Once oviposition behavior commenced, however, it was almost always completed without interruption by other searching females. The first experiment (Table 1) showed that medflies had strategies for oviposition and distribution of egg which differed with fruit type. The results suggested that fruit size was the important factor in determining the number of eggs per oviposition.

Puncturing of fruits facilitated oviposition (Table 2). Flies on punctured fruit quickly located the punctures and oviposited while those on non-punctured fruit made repeated attempts to penetrate the epidermis, most often without success. Chemical stimulation may have played a role in the heightened oviposition levels for punctured fruits. Many tephritid species regularly take advantage of punctures in fruit. *Dacus tryoni* uses existing punctures for up to 70% of oviposition in hard shiny fruit and 20% in soft bumpy fruit (Pritchard, 1969). *Dacus dorsalis* has been observed to use punctures made by medflies (Christenson & Foote, 1960).

The difference of mean egg clutch size for grape and apple was 3.6 fold (3.9 versus 14.0) when each oviposition was documented (Table 3). The values departed from those from the group exposures (Table 1) – but in a consistent direction – which gave a 4.5-fold difference (1.7 versus 7.7). The flies in the group exposures were not prevented from ovipositing into pre-existing punctures made by predecessors. Oviposition into punctures probably

resulted in lowered numbers of eggs per oviposition (cf. Table 2). In the individual exposures punctures without eggs (33 of 108 punctures for grapes) were excluded from calculations. In the group exposures such apparent ovipositions would have been recorded as true ovipositions.

The tests with parafilm covered fruits and spheres showed that clutch size was influenced more by fruit size than by fruit type (Table 4). Trials with a greater variety of fruits would be needed to determine if chemistry played an important role in regulating clutch size. However, given the polyphagous nature of the medfly, it seems most likely that fruit size is the major determiner of clutch size in this species.

Zusammenfassung

Ceratitis capitata: Einfluss der Fruchtgrösse auf die Zahl der Eier in einer Eiablage

Einem Laboratoriumsstamm von *Ceratitis capitata* (Wiedemann) wurden Trauben, Pflaumen, Äpfel und Pfirsiche zur Eiablage vorgelegt. Der Fruchtdurchmesser war stark korreliert mit der Eizahl pro Eiablage. Die Grösse der Eihaufen war $3,9 \pm 0,3$ bei Trauben (20 mm) und $14,0 \pm 0,7$ bei Äpfeln (70 mm). Wenn geschälte und mit Parafilm® eingehüllte ganze Früchte und Fruchtscheiben vorgelegt wurden, war die Fruchtgrösse wichtiger als der Fruchttyp für die Grösse der Eiablage. Eiablagen, bei denen die Fruchthaut durchbohrt werden musste, waren grösser als Eiablagen durch Parafilm oder in perforierte Früchte.

References

- Boller, E. F., 1968. An artificial oviposition device for the European cherry fruit fly, *Rhagoletis cerasi*. J. Econ. Entomol. 61: 850-852.
- Carey, J. R., 1984. Host-specific demographic studies of the Mediterranean fruit fly, *Ceratitidis capitata* (Wied.). Ecol. Entomol. 9: 261-270.
- Christenson, L. D. & R. H. Foote, 1960. Biology of fruit flies. Ann. Rev. Entomol. 5: 171-192.
- Féron, M., 1962. L'instinct de reproduction chez la Mouche méditerranéenne des fruits *Ceratitidis capitata* Wied. (Dipt. Trypetidae). Comportement sexuel. Comportement de ponte. Rev. Pathol. Vég. Entomol. Agric. France 41: 1-129.
- Fitt, G. P., 1984. Oviposition behaviour of two tephritid fruit flies *Dacus tryoni* and *Dacus jarvisi*, as influenced by the presence of larvae in the host fruit. Oecologia (Berlin) 62: 37-46.
- Hagen, K. S., W. A. Allen & R. L. Tassan, 1981. Mediterranean fruit fly: the worst may be yet to come. Calif. Agric. (March-April): 5-7.
- Nakagawa, S., R. J. Prokopy, T. T. Y. Wong, J. R. Ziegler, S. M. Mitchell, T. Urugo & E. J. Harris, 1978. Visual orientation of *Ceratitidis capitata* flies to fruit models. Entomol. exp. appl. 24: 193-198.
- Pritchard, G., 1969. The ecology of a natural population of Queensland fruit fly, *Dacus tryoni* Aust. J. Zool. 17: 293-311.
- Prokopy, R. J. & J. Koyama, 1982. Oviposition site partitioning in *Dacus cucurbitae*. Entomol. exp. appl. 31: 428-432.
- Prokopy, R. J. & B. D. Roitberg, 1984. Foraging behavior of true fruit flies. American Scientist 72: 41-49.
- Prokopy, R. J., P. T. McDonald & T. T. Y. Wong, 1984. Interpopulation variation among *Ceratitidis capitata* flies in host acceptance pattern. Entomol. exp. appl. 35: 65-69.
- Prokopy, R. J., J. R. Ziegler, T. T. Y. Wong, 1978. Deterrence of repeated oviposition by fruit-marking pheromone in *Ceratitidis capitata* (Diptera:Tephritidae). J. Chem. Ecol. 4: 55-63.
- Sanders, W., 1962. Das Verhalten der Mittelmeerfruchtfliege *Ceratitidis capitata* Wied. bei der Eiablage. Z. Tierpsychol. 19: 1-28.
- Sanders, W., 1968a. Die Eiablagehandlung der Mittelmeerfruchtfliege *Ceratitidis capitata* Wied. Ihre Abhängigkeit von Grösse und Dichte der Frucht. Z. Tierpsychol. 25: 1-21.
- Sanders, W., 1968b. Die Eiablagehandlung der Mittelmeerfruchtfliege *Ceratitidis capitata* Wied. Ihre Abhängigkeit von Farbe und Gliederung des Umfeldes. Z. Tierpsychol. 25: 588-607.
- Sanders, W., 1969. Die Eiablagehandlung der Mittelmeerfruchtfliege *Ceratitidis capitata* Wied. Ihre Abhängigkeit von der Oberflächen und Innenfeuchte der Frucht. Z. Tierpsychol. 26: 236-242.
- Tanaka, N., 1965. Artificial egg receptacles for three species of tephritid flies. J. Econ. Entomol. 58: 177-178.
- Weis, A. E., P. W. Price & M. Lynch, 1983. Selective pressures on clutch size in the gall maker *Asteomyia carbonifera*. Ecology 64: 688-695.
- Wong, T. T. Y., J. I. Nishimoto & M. Mochizuki, 1983. Infestation patterns of Mediterranean fruit fly and the oriental fruit fly (Diptera:Tephritidae) in the Kula area of Maui, Hawaii. Environ. Entomol. 12: 1031-1039.

Accepted: October 26, 1984.